

DESCRIPTIONS OF A NEW GENUS AND TWO NEW SPECIES OF VIVIPARID SNAILS
(MOLLUSCA: GASTROPODA: VIVIPARIDAE) FROM THE EARLY CRETACEOUS
(MIDDLE-LATE ALBIAN) GRIMAN CREEK FORMATION OF LIGHTNING RIDGE,
NORTHERN NEW SOUTH WALES

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Fossil gastropods belonging to the family Viviparidae (Caenogastropoda (Prosobranchia)) are described from the Early Cretaceous (middle-late Albian) Griman Creek Formation of Lightning Ridge, northern New South Wales. From our research, this is the earliest definitive record of non-marine gastropods from Australia and amongst the oldest viviparid material in the world recorded to date. A new genus and two new species are described, and other material attributable to the extant genus *Notopala* is recorded. Implications for the current distribution of the Viviparidae are addressed.

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Opalised fossils have long been known from the Lower Cretaceous (middle-late Albian) freshwater deposits of the Griman Creek Formation, Lightning Ridge, New South Wales (Smith 1999). To date, much of the published work has focused on fish (Kemp 1991; Kemp & Molnar 1981) and terrestrial tetrapod remains (Archer et al 1985; Flannery et al 1995; Molnar 1980a, 1980b, 1991; Molnar & Galton 1986; Rich et al 1989) with relatively few reports (Deuman et al 1992; McMichael 1957; Smith 1999) summarising the vast quantities of invertebrate material recovered from the area. The recent opportunity to examine Lightning Ridge gastropod specimens (brought to our attention by Ben Kear, South Australian Museum, as part of an ongoing assessment of vertebrate and invertebrate fossil material from the locality) from the collections of the Australian Museum, Sydney, and several private individuals has prompted a systematic appraisal of the gastropods within the material recovered. This study describes specimens attributable to the family Viviparidae (Caenogastropoda (= Prosobranchia)), including a new genus and two new species. Indeterminate material belonging to the extant genus *Notopala* is also recorded, and the implications for

distribution of extant viviparid taxa are discussed.

The Viviparidae is a cosmopolitan group of freshwater caenogastropods, characterised by medium- to large-sized turbiniform shells which possess a rounded body whorl; moderately high, pointed spire; wide, round aperture; and sub-spiral, horny operculum (Smith 1992). The current Australian distribution of the group is limited to a few species occurring in the large drainage basins that span much of the arid centre and northern tropical regions of the continent.

The fossil record for Viviparidae is known from the Jurassic to Recent (*Viviparus* Montfort, 1810), with a tentative report based on an internal shell (?*Bernicia* Cox, 1927) mould (possibly of marine origin) from the Lower Carboniferous of England (Brookes-Knight et al 1960). Within Australia there are few records of fossil viviparids. Etheridge (1902) described the earliest potential Australian taxon, *Viviparus* (?) *alba-scopularis* Etheridge (also noted by Newton (1915)) from the Aptian marine deposits of the Doncaster Member (Wallumbilla Formation *sensu* Burton & Mason 1998), White Cliffs, New South Wales. This specimen is currently under examination by the authors and at present is regarded as being of unclear viviparid affinity. Cotton (1935a) erected

a species of *Notopala* (*N. wanjacalda*) from late Pleistocene sediments along the Murray River near Sunnyside, South Australia, and also noted a second taxon (*Notopala* sp.) from the same deposits, which showed strong similarity to the extant *N. hanleyi* (Frauenfeld, 1862). Viviparid snail shells from Early Cretaceous deposits in the Lightning Ridge area were recorded but not described by Dettman et al (1992) and Smith (1999); the latter also recorded possible representatives of the Naticidae, Thiaridae and Ellobiidae. Few other Australian non-marine gastropod fossils (all of Tertiary age) have been recorded (Archer et al 1994; Arena, 1997; Chapman 1937; McMichael 1968).

MATERIALS AND METHODS

All specimens described herein are derived from the Lightning Ridge opal fields (exact mine localities from which these specimens originated are unknown), Surat Basin, northwestern New South Wales. The opal-bearing sediments in this area form part of the Griman Creek Formation, a unit dated as middle-late Albian in age (Dettman et al 1992). The deposit predominantly reflects a coastal plain facies (Burger 1988; Dettman et al 1992) situated in an Early Cretaceous high latitude zone (~70° S, Embleton 1984). Invertebrate fossils, plant root impressions and vertebrate taphonomy suggest a freshwater estuarine to lacustrine setting (Dettman et al 1992; Molnar 1980a). Palaeoclimatic indicators imply strongly seasonal conditions with sea-level isotopic palaeotemperatures in the Eromanga Basin / Surat Basin regions ranging from 11.9°C (northeast) to 16.3°C (southwest) (Dettman et al 1992; Stevens & Clayton 1971).

Designation of parietal fold position on the specimens was achieved by positioning the fold within the aperture on a 360° compass setting when a vertical line through the axis, juxtaposed to the column, is intersected by a horizontal line corresponding to the midpoint of the aperture. The adapical axis above the point of intersection is taken as zero degrees. The diameters of all shells were measured following the method of Boycott (1928) and are defined as 'the greatest dimension that can be found starting with the edge of the lip to a point on the opposite side of the shell on the last whorl'. To enable extrapolation of the numbers of missing whorls, the incremental angle of the shells was judged by drawing a line so as to touch each of the

present whorls across each side of the shell; the point at which they met was assessed as being approximately the original apex of the shell (Cox 1960). All specimens are deposited in the Australian Museum (AM), Sydney. All specimens were prepared using a diamond drill-bit attached via a flexible lead to a high-speed rotary motor. Shell measurements were made to the nearest 0.05 mm using dial calipers.

SYSTEMATICS

Class GASTROPODA

Subclass ORTHOGASTROPODA

Superorder CAENOGASTROPODA

Order ARCHITAENIOGLOSSA

Superfamily AMPULLARIOIDEA

Family VIVIPARIDAE Gray, 1847

Diagnosis

Medium to large dextral, turbiniform shells, body whorl rounded, spire moderately high, pointed; aperture wide, round, parietal fold present or absent; operculum horny, subspiral (modified after Smith 1992).

Remarks

The above diagnosis follows Smith (1992), modified to accommodate the presence of a parietal fold in the new genus described below. Viviparid snails are, as their name suggests, viviparous (live bearing) and are found in both lotic and lentic systems throughout the world (Browne 1978). Within Australia the family is currently represented by the extant native genera *Notopala*, *Larina* and *Centropala* (Smith 1992). A species accidentally introduced from Asia, *Bellamyia heudei guangdongensis* (Kobelt, 1906), recorded by Shea (1994) as established in New South Wales, is not considered part of the Australian fauna in this study. The Australian members of the family have undergone substantial revision over many years (Cotton 1935a, 1935b; Sheldon & Walker 1993; Stoddart 1982); the use of intraspecific shell variation and morphometric data by recent authors has resulted in a substantial reduction in the numbers of accepted species. Shell colouring and pattern and the form of the operculum, which are important characters in

determining generic placement in this family, are characters lost in most fossils.

The present specimens from Lightning Ridge are over 100 million years old (Albian [108–97.5 Ma]) and totally opalised. While sculpturing on some specimens has been preserved, colour bands and opercula have not; therefore, only structural shell characters could be used to assign them to taxa. Two major factors have been taken into account before deciding to place them in Viviparidae — the shell morphology, which fits within the currently accepted diagnosis of the family with only slight modification (the presence of the parietal fold in the two new species); and the freshwater depositional environment from which they originated. Whilst all the specimens can be accommodated within the family Viviparidae, those possessing a parietal fold cannot be assigned to any currently recognised genus and are considered to belong to a new genus which is described below. Direct comparisons between species, living or fossil, are few (Brown 1980); however, due to the lack of colour patterns and opercula as well as soft parts in these fossils, the only remaining methods are based on morphology. Therefore, we have applied parts of the morphometric data gathered by Sheldon and Walker (1993) to justify the placement of these specimens within Viviparidae, and in one case in the extant genus *Notopala*, and to offer a method of comparison between extant and extinct species. None of the data comparisons

are in any way intended to suggest relationships between members of either the *Notopala* sp. presented here or the new genus and any extant species.

Genus *Albianopalin* gen. nov.

Diagnosis

Shell dextral, thick, solid, globose to subglobose, ventricose, three–five whorls, subumbilicate; aperture subovate, large, approximately equal to height of spire; parietal fold present, simple. Operculum unknown.

Type species

Albianopalin benkeari sp. nov.

Etymology

From the combination of *Albian*, n. referring to age of the Lower Cretaceous opal-bearing deposits of the Grimian Creek Formation, and *opalin*, Middle English, from *opalus*, Latin, alteration of Greek *opallios*, for 'opal'.

Remarks

While this new genus has similarities to *Notopala* (Cotton, 1935b), *Albianopalin* gen. nov. is easily separated from *Notopala* and all other genera within the family by the presence of a parietal fold in the basal lip, currently a feature unique to this genus within the family.

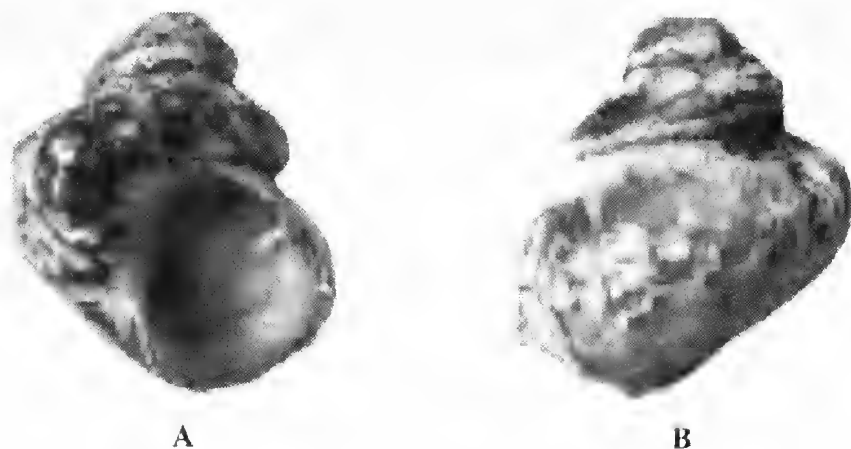


FIGURE 1. AMF122185 *Albianopalin benkeari* sp. nov. in A, apertural and B, dorsal views.

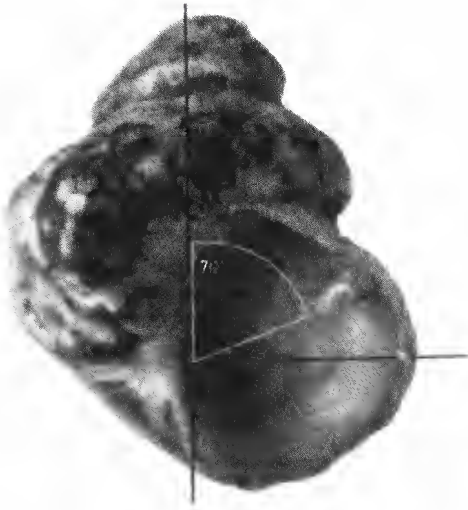


FIGURE 2. AMF122185 *Albanopalina benkeari* sp. nov. in apertural view showing angle of parietal fold.

Albanopalina benkeari sp. nov. (Figs 1, 2, Appendix)

Diagnosis

With the features of the genus; parietal fold simple, 70° from vertical axis.

Type specimen

Holotype: AMF122185 (Figs 1, 2, Appendix)

Locality and horizon

Lightning Ridge opal fields (precise site within the opal fields unknown), northern New South Wales, Surat Basin, Griman Creek Formation, middle-late Albian.

Description

Shell 17.7 mm high, 16.4 mm maximum diameter, dextral, turbiniform, subglobose. Teleconch with three complete whorls and broken parts, pointing to the possible presence of further whorls. Whorls impressed. Relatively evenly spaced spiral prosocyrct ornamentation present on many areas of teleconch. Aperture large (10.85 mm high), round; basal outer lip varicose with no evidence of eversion. A single, triangulated parietal fold (3.0 mm long, 1.0 mm wide, 2.0 mm deep) present on upper surface of basal lip, deepest side facing adaperturally (Fig. 2).

Etymology

Named for Ben Kear, for his assistance in this study.

Remarks

Holotype unique. The position of the parietal fold separates *A. benkeari* sp. nov. from the other new species described below. The holotype specimen is undistorted, but the spire is incomplete. Extrapolation from the spire angle indicates that there may have been at least four and as many as five complete whorls originally. Being opalised, the state of preservation of the holotype is very good, with much of its detailed surface ornamentation preserved.

Albianopalina lizsmithae sp. nov. (Figs 3, 4, Appendix)

Diagnosis

With the features of the genus; parietal fold simple, 112° from the vertical.

Type specimen

Holotype: AMF122186 (Figs 3, 4, Appendix)

Locality and horizon

Lightning Ridge opal fields (precise site within the opal fields unknown), northern New South Wales, Surat Basin, Griman Creek Formation, middle-late Albian.

Description

Shell, 15.1 mm high, 12.9 mm maximum diameter, dextral, turbiniform, subglobose. Teleconch with two complete whorls and broken parts, pointing to the possible presence of further whorls. Whorls impressed. This particular specimen has undergone some dorsoventral compression which has resulted in distortion, especially at base of final whorl. Aperture large (9.95 mm high), round; basal outer lip varicose with no evidence of eversion. A single, basal parietal fold (3.75 mm long, 2.3 mm wide, 2.2 mm deep) is present on surface of basal lip, deepest side facing adaperturally (Fig. 4). Spiral prosocyrct ornamentation present on parts of teleconch, especially proximal to aperture.

Etymology

We name this species for our colleague Elizabeth (Liz) Smith of the Australian Museum (AM), for her assistance in this study.



FIGURE 3. AMF122186 *Albanopalin lizsmithae* sp. nov. in A, apertural and B, dorsal views.

Remarks

Holotype unique. The position of the parietal fold separates *A. lizsmithae* sp. nov. from *A. benkeari* sp. nov. as described above. The holotype has undergone moderate dorsoventral compression, resulting in the specimen appearing stretched. Like *A. benkeari* sp. nov., the spire is incomplete, and extrapolation from the spire angle indicates that there originally may have been at least four and as many as five complete whorls. Being opalised and having damage to parts of the surface of the telecone, the state of preservation is good enough to preserve some of its detailed surface ornamentation.

Genus *Notopala* (Cotton, 1935b)

Type specimen

Type species: *Paludina hanleyi* (Frauenfeld, 1864) by original designation.

Diagnosis

Shell dextral, globose-conic, subumbilicate, five whorls, ventricose to angulate below the periphery; aperture subovate, large, about equal to height of spire; parietal fold absent; operculum corneous.

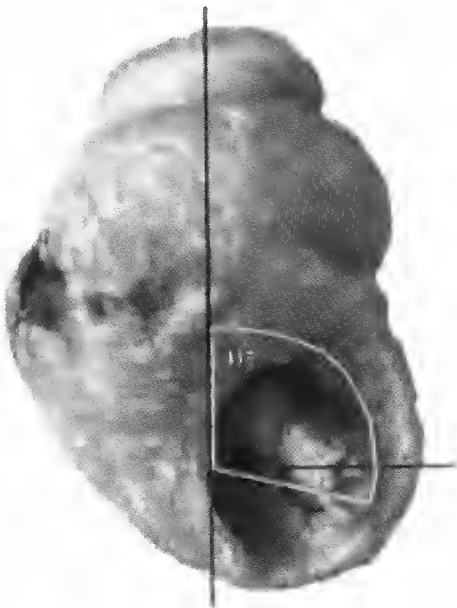


FIGURE 4. AMF122186 *Albanopalin lizsmithae* sp. nov. in apertural view showing angle of parietal fold.

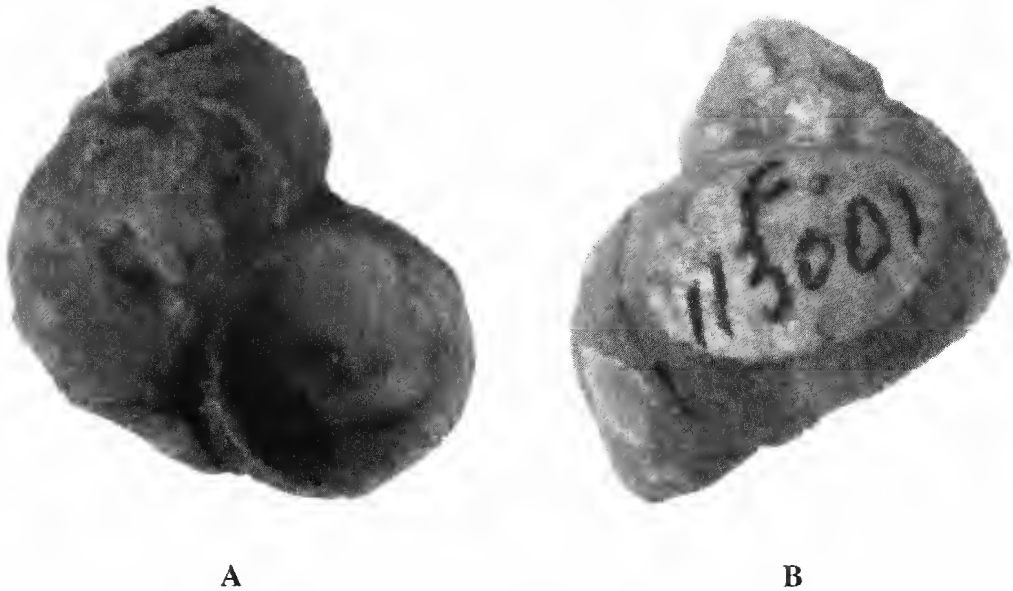


FIGURE 5. AMF13001 *Notopala* sp. in A, apertural and B, dorsal views.

Remarks

These specimens are extremely significant. Until their discovery, none of the currently living native Australian viviparid genera were known from deposits older than Plio-Pleistocene. This temporal range is now extended back to the Lower Cretaceous (middle-late Albian). It is also interesting to note that another living species, the lungfish *Neoceratodus forsteri*, has been recorded from the Griman Creek Formation of Lightning Ridge (Kemp & Molnar 1981).

Notopala sp. (Fig. 5, Appendix)

Referred material

AMF13001 (Fig. 5), AMF122166–AMF122184 (not figured herein).

Locality and horizon

Lightning Ridge opal fields (precise site within the opal fields unknown), northern New South Wales, Surat Basin, Griman Creek Formation, middle-late Albian.

Description

Shell dextral, turbiniform, subglobose. Teleconch with two to three complete impressed whorls; the incremental angle of the shell indicates that there were originally four or five whorls. Aperture large, round; basal outer

lip varicose with no evidence of eversion.

Remarks

There is considerable variation in size, state of preservation, degree of corrosion and/or damage to the shells, opalisation, amount of matrix deposition on the shells, completeness of the aperture and presence/absence of ornamentation. We have not described these specimens as a new species at this stage. We feel that the exact taxonomic position of this material compared with other species in the genus requires further study. The preceding table (Table 1), diagram (Fig. 6, modified from Sheldon & Walker 1993) and graph (Fig. 7) show measurements of shell characters for each of the living Australian species of *Notopala*, and illustrate morphometric similarity of the specimens of *Albianopalin* nov. sp. as well as *Notopala* sp. described here to existing members of the genus. However, the specimens of *Notopala* sp. vary greatly in their physical condition, and it has not been possible to take the full range of measurements from each of the 20 specimens being studied. The reason for the inclusion of this data is not to demonstrate any relationship between extant species and the specimens from Lightning Ridge, but to show that the physical characteristics of the new material (*Albianopalin* sp. nov. and *Notopala* sp.) fit within the parameters for inclusion in the family Viviparidae.

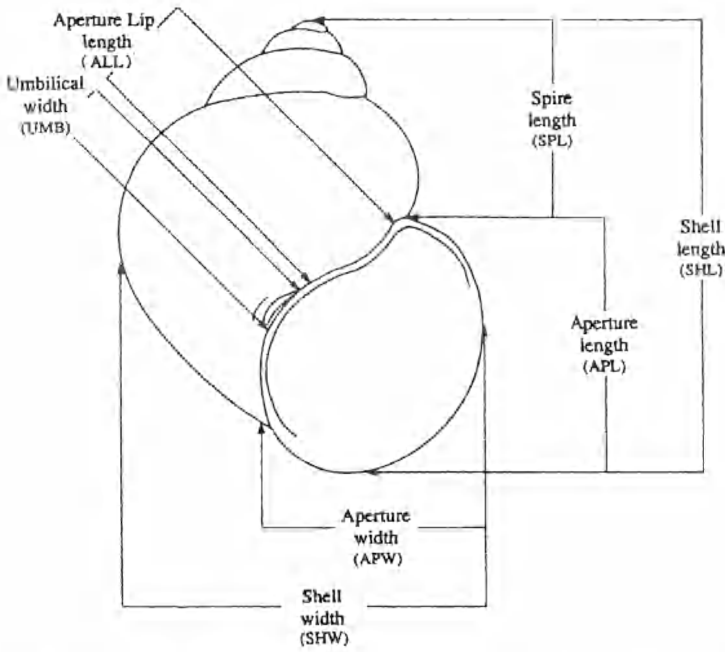


FIGURE 6. Diagram illustrating measurement parameters used in the morphometric analysis (modified from Sheldon & Walker 1993).

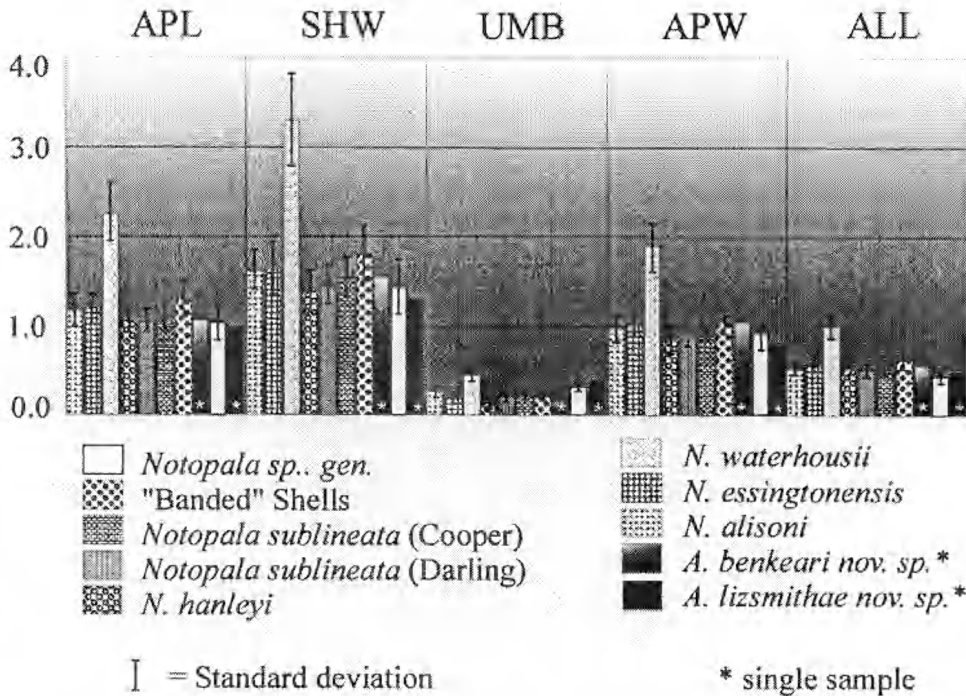


FIGURE 7. Histogram showing results of morphometric analysis. Taxa include living species of *Notopala* (modified from Sheldon & Walker 1993), *Notopala* sp. (AMF13001, AMF122185–122184), *Albianopalin benkeari* (AMF122185) and *A. lizsmithae* (AMF122186).

TABLE 1. Mean shell measurements (mm) for various living species of *Notopala* (*modified from Sheldon & Walker 1993) compared with those for *Notopala* sp. (AMF13001, AMF122185–122184), *Albianopalin benkeari* (AMF122185) and *A. lizsmithae* (AMF122186). Because not all specimens of *Notopala* sp. were complete, the number (n) of specimens used for each individual parameter is indicated separately. Standard deviation (SD) rows were not included for *A. benkeari* and *A. lizsmithae* as only a single specimen has currently been recovered for each of these taxa. Abbreviations: SHL, shell length; APL, apertural length; SHW, shell width; UMB, umbilical width; APW, aperture width; SPL, spire length; ALL, aperture lip length.

Species	Number	SHL	APL	SHW	UMB	APW	SPL	ALL
* <i>N. alisoni</i> (Brazier, 1979)	20	21.59	11.91	16.3	02.59	09.77	14.78	05.35
		SD 0.086	0.039	0.054	0.014	0.034	0.064	0.015
* <i>N. essingtonensis</i> (Frauenfeld, 1862)	20	21.70	12.00	16.58	1.96	10.10	14.47	6.11
		SD 0.082	0.038	0.067	0.016	0.038	0.067	0.025
* <i>N. waterhousii</i> (Adams & Angus, 1864)	10	38.59	22.84	33.14	4.63	18.88	25.01	10.02
		SD 0.209	0.105	0.164	0.024	0.087	0.131	0.043
* <i>N. hanleyi</i> (Frauenfeld, 1862)	42	16.67	10.50	13.83	1.29	8.52	11.00	5.57
		SD 0.520	0.026	0.036	0.00	0.025	0.037	0.013
* <i>N. sublineata</i> (D) (Conrad 1850)	28	18.32	10.84	14.53	2.05	9.21	12.04	5.24
		SD 0.063	0.024	0.040	0.012	0.026	0.039	0.016
* <i>N. sublineata</i> (C) (Conrad 1850)	35	19.46	11.06	15.52	2.21	8.89	12.59	4.93
		SD 0.058	0.027	0.039	0.010	0.018	0.040	0.009
*'Banded' shells	15	22.15	13.18	18.10	2.06	10.69	14.6	6.42
		SD 0.110	0.053	0.008	0.011	0.045	0.079	0.029
<i>Notopala</i> sp.	20	–	10.35 (19)	14.43 (20)	3.24 (10)	9.20 (15)	–	4.71 (9)
		SD –	2.563	3.053	0.616	1.80	–	1.071
<i>A. benkeari</i>	1	17.7	10.85	16.4	3.35	9.85	–	6.2
<i>A. lizsmithae</i>	1	15.1	9.95	12.9	3.4	8.15	–	4.4

DISCUSSION

Albianopalin benkeari sp. nov., *A. lizsmithae* sp. nov. and *Notopala* sp. share the distinction of being the three oldest known definitively assigned members of the Viviparidae in Australia and thus serve to extend the range of the family in this region back to at least the uppermost Early Cretaceous. Since the family is confidently known from the Jurassic to Recent in Europe, Viviparidae therefore appears to be an ancient pre-Jurassic group of probable Pangean origin. By the Cretaceous, the family had diversified within the Gondwanan region into a range of endemic genera and species.

While there are numerous Cretaceous records of freshwater bivalves from Australia (Dettman et al 1992; Hocknull 1997; Jell & Duncan 1986; Ludbrook 1985; McMichael 1957), there are very few for non-marine gastropods from the same period. The reasons for this apparent absence are unknown, but could be related to preservational biases (with shells rapidly breaking up or dissolving after death). Another possibly reason could be a lack of gastropod species due to poor tolerance of the strongly seasonal near-freezing

climatic conditions which characterised many Australian high latitude depositional environments during the Early Cretaceous.

The implications of this study, combined with subsequent investigations, could eventually demonstrate a Gondwanan and possibly Australian radiation for many of the species living around the globe today.

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REFERENCES

- Archer, M, Flannery, TF, Ritchie, A & Molnar, RE. 1985. First Mesozoic mammal from Australia. *Nature* **318**: 363–366.
- Archer, M, Hand, S & Godthelp, H. 1994. 'Riversleigh: the Story of Animals in Ancient Rainforests of Inland Australia'. Reed Books: Sydney.
- Arena, DA. 1997. The palaeontology and geology of Dunsinane Site, Riversleigh. *Memoirs of the Queensland Museum* **41**: 171–179.
- Boycott, AE. 1928. Conchometry. *Proceedings of the Malacological Society of London* **18**: 8–31
- Brookes-Knight, J, Batten, RL, Yochelson, EL & Cox, LR. 1960. Supplement Paleozoic and some Mesozoic Caenogastropoda and Opisthobranchia. In 'RC Moore (ed). Treatise on Invertebrate Paleontology, Part I Mollusca 1', pp. 1310–1331. University of Kansas Press: Lawrence, Kansas, USA.
- Brown, DS. 1980. 'Freshwater Snails of Africa and Their Medical Importance'. Taylor & Francis: London.
- Browne, RA. 1978. Growth, mortality, fecundity, biomass and productivity of four lake populations of the Prosobranch snail, *Viviparus georginaus*. *Ecology* **59**: 742–750.
- Burger, D. 1988. Early Cretaceous environments in the Eromanga Basin; palynological evidence from GSQ Wyandra-1 corehole. *Memoirs of the Association of Australasian Palaeontologists* **5**: 173–186.
- Burton, GR & Mason, AJ. 1998. Controls on opal localisation in the White Cliffs area. *Quarterly Notes, Geological Survey of New South Wales* **107**: 1–11.
- Chapman, F. 1937. Chert limestone with *Planorbis*, from the Mount Elder Range, Western Australia. *Proceedings of the Royal Society of Victoria* **50**: 59–68.
- Cotton, BC. 1935a. Recent Australian Viviparidae and a fossil species. *Records of the South Australian Museum* **5**: 339–344.
- Cotton, BC. 1935b. The Australian viviparous river snails. *Victorian Naturalist* **52**: 96–99.
- Cox, LR. 1960. Gastropoda. General characteristics of the Gastropoda. In RC Moore (ed). 'Treatise on Invertebrate Palaeontology, Part I Mollusca 1', pp. 184–1169. University of Kansas Press: Lawrence, Kansas, USA.
- Dettman, ME, Molnar, RE, Douglas, JG, Burger, D, Fielding, C, Clifford, HT, Francis, J, Jell, P, Rich, T, Wade, M, Rich, PV, Pledge, N, Kemp, A & Rozefelds, A. 1992. Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. *Cretaceous Research* **13**: 207–262.
- Etheridge, R. 1902. A monograph of the Cretaceous invertebrate fauna of New South Wales. *Memoirs of the Geological Survey of New South Wales* **11**: 1–98.
- Embleton, BJJ. 1984. Australia's global setting: past global settings. In JJ Veivers (ed). 'Phanerozoic Earth History of Australia', pp. 11–17. Clarendon Press: Oxford.
- Flannery, TF, Archer, M, Rich, TH & Jones, R. 1995. A new family of monotremes from the Cretaceous of Australia. *Nature* **377**: 418–420.
- Hocknull, S. A. 1997. Cretaceous freshwater bivalves from Queensland. *Memoirs of the Queensland Museum* **42**: 223–226.
- Jell, PA & Duncan, PM. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoirs of the Association of Australasian Palaeontologists* **3**: 111–205.
- Kemp, A. 1991. Australian Cenozoic and Mesozoic lungfish. In P Vickers-Rich, JM Monaghan, RF Baird & TH Rich (eds). 'Vertebrate Palaeontology of Australasia', pp. 465–489. Pioneer Design Studio, Monash University: Melbourne.
- Kemp, A & Molnar, RE. 1981. *Neoceratodus forsteri* from the Lower Cretaceous of New South Wales, Australia. *Journal of Paleontology* **55**: 211–217.
- Ludbrook, NH. 1985. Mesozoic non-marine Mollusca (Pelecypoda: Unionidae) from the north of South Australia. *Transactions of the Royal Society of South Australia* **84**: 139–147.
- McMichael, DF. 1957. A review of fossil freshwater mussels (Pelecypoda: Unionidae) of Australasia. *Proceedings of the Linnean Society of New South Wales* **81**: 222–242.
- McMichael, DF. 1968. Non-marine Mollusca from Tertiary rocks in Northern Australia. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* **80**: 133–160.
- Molnar, RE. 1980a. Procoelous crocodile from the Lower Cretaceous of Lightning Ridge N.S.W. *Memoirs of the Queensland Museum* **20**: 65–75.
- Molnar, RE. 1980b. Australian late Mesozoic terrestrial tetrapods: some implications. *Memoirs de les Société Géologique de France* **139**: 131–143.
- Molnar, RE. 1991. Fossil reptiles in Australia. In P, Vickers-Rich, JM Monaghan, RF Baird & TH Rich (eds). 'Vertebrate Palaeontology of Australasia', pp. 605–702. Pioneer Design Studio, Monash University: Melbourne
- Molnar, RE & Galton, PM. 1986. Hypsilophodontid dinosaurs from Lightning Ridge, New South Wales. *Geobios* **19**: 231–239.
- Newton, RB. 1915. On some molluscan remains from

- the opal deposits (Upper Cretaceous) of New South Wales. *Proceedings of the Malacological Society of London* **11**: 217–235.
- Rich, TH, Flannery, TF & Archer, M. 1989. A second Cretaceous mammalian specimen from Lightning Ridge, New South Wales, Australia. *Alcheringa* **13**: 85–88.
- Shea, M. 1994. The Chinese viviparid snail *Bellamya heudei guangdongensis* (Kobelt, 1906) in Australia (Prosobranchia: Viviparidae). *Molluscan Research* **15**: 3–11.
- Smith, BJ. 1992. Non-marine Mollusca. In WWK Houston (ed), 'Zoological Catalogue of Australia' Vol. 8, pp. 1–398. Australian Government Publishing Service: Canberra.
- Smith, E. 1999. 'Black opal fossils of Lightning Ridge'. Kangaroo Press: Sydney.
- Sheldon, F & Walker, KF. 1993. Shell variation in Australian *Notopala* (Gastropoda: Prosobranchia: Viviparidae). *Journal of the Malacological Society of Australia* **14**: 59–71.
- Stevens, GR & Clayton, RN. 1971. Oxygen isotope studies on Jurassic and Cretaceous belemnites from New Zealand and their biogeographic significance. *New Zealand Journal of Geology and Geophysics* **14**: 829–897.
- Stoddart, JA. 1982. Western Australian viviparids (Prosobranchia: Mollusca). *Journal of the Malacological Society of Australia* **5**: 167–173.

APPENDIX

Measurements (mm) of all Lightning Ridge gastropod specimens used in this study (AMF13001, AMF122166–AMF122186). Abbreviations: SHL, shell length; APL, apertural length; SHW, shell width; UMB, umbilical width; APW, aperture width; SPL, spire length; ALL, aperture lip length. Spire length measurements are omitted owing to incomplete apices in all specimens sampled.

Specimen	SHL	APL	SHW	UMB	APW	ALL
1. AMF122185 (type <i>A. benkeari</i>)	17.70	10.85	16.40	3.35	9.85	6.20
2. AMF122186 (type <i>A. lizsmithae</i>)	15.10	9.95	12.90	3.40	8.15	4.40
3. AMF13001 (<i>Notopala</i> sp.)	19.25	12.00	17.30	3.75	11.10	5.02
4. AMF122166	17.65	11.05	14.50	–	8.55	–
5. AMF122167	14.37	8.75	12.75	8.50	–	–
6. AMF122168	11.60	–	11.85	2.30	7.80	3.35
7. AMF122169	15.62	8.80	12.45	3.00	–	5.00
8. AMF122170	12.60	8.80	11.65	3.00	7.65	4.35
9. AMF122171	19.00	13.25	19.90	–	12.20	–
10. AMF122172	20.42	12.10	17.20	4.20	–	6.00
11. AMF122173	18.00	11.05	16.20	3.90	9.80	–
12. AMF122174	17.92	11.20	15.55	–	11.15	–
13. AMF122175	19.82	12.63	17.85	3.35	–	–
14. AMF122176	19.35	11.10	16.75	–	10.50	–
15. AMF122177	19.57	12.65	17.50	–	11.70	–
16. AMF122178	18.55	10.05	15.15	–	–	–
17. AMF122179	17.95	11.30	15.20	3.80	9.60	4.80
18. AMF122180	10.22	6.50	9.00	–	–	6.00
19. AMF122181	6.92	7.20	9.40	2.60	6.15	3.60
20. AMF122182	9.32	6.50	8.75	2.35	5.60	3.15
21. AMF122183	17.80	11.70	16.00	–	9.80	–
22. AMF122184	–	16.10	10.10	13.40	–	8.30